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BIOLOGICAL BULLETIN

SOME NEW TYPES OF CHROMOSOME DISTRIBUTION AND THEIR RELATION TO SEX. *Continued.*

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GENERAL.

The Chromosome Nucleoli.

The term "chromosome nucleolus" has come to mean, in a general sense, any chromosome, which remains condensed during the growth period. Under this heading, then, I shall discuss briefly the origin, valence and history of four different classes of chromosomes, namely: the accessory chromosome, idiochromosomes, m-chromosomes and differential chromosomes.

Henking ('91) observed a deeply staining body in the growth period of the primary spermatocytes of *Pyrrhocoris*, but did not detect its origin. He did recognize its chromatic nature and its unequal distribution in the second division, whereby one spermatozoon received one more chromatin element than the other. Montgomery ('98) was the first to detect that the accessory chromosome (chromosome nucleolus) was nothing more than a spermatogonial chromosome which differs in its behavior from the others, but he believed that it divided in both divisions. Paulmier, in his work on *Anasa tristis* ('99) described an accessory chromosome or what he called a "chromatin-nucleolus," which he thought originated at the time of synapsis by the union of two small spermatogonial chromosomes, divided in the first maturation division, but passed over undivided in the second. Montgomery ('01) discarded his former interpretation and accepted that of Paulmier. In the case of *Syromastes* ('04) and *Pyrrhocoris* ('06), Gross believed the accessory chromosome to arise by the fusion of two spermatogonial chromosomes which

divided in one division but not in the other. According to these interpretations, then, the accessory chromosome would be bivalent.

McClung, however ('01), maintained the accessory to be univalent. Wilson ('05 and '06) has shown in the Hemiptera heteroptera that Paulmier ('99) and Montgomery ('01) were wrong in their interpretation of the origin of the accessory chromosome, that the small bivalent divides in both divisions, and that the accessory chromosome is a univalent spermatogonial chromosome which divides in only one division, and this was confirmed by Montgomery ('06) in opposition to his earlier conclusion.

The results of Gross ('04 and '06) have been more or less of a hindrance to the correct interpretation of the accessory chromosome. Wilson ('09) again has shown that Gross was mistaken in the case of *Pyrrhocoris* and that the accessory chromosome is here univalent. He confirms, however, Gross's results on the male cells of *Syromastes*. The spermatogonial number is even (22), and the accessory chromosome is here, in fact, bivalent, but it divides in only one division. Gross figured the same number of chromosomes in both male and female cells, but Wilson inferred (not having material) that the oögonial cells would show 24 chromosomes, since the accessory chromosome is bivalent. In an addendum to his last paper ('09b) Wilson states that his inference has proven true and that the female cells of *Syromastes* have, in fact, 24 chromosomes. In principle, therefore, *Syromastes* conforms to those forms in which the accessory chromosome is univalent.

Another contradiction occurs in the work of Foot and Strobell ('07) on *Anasa tristis*, who assert that the densely staining body in the rest stages of the spermatocytes is a true nucleolus and not a chromosome nucleolus formed by the accessory chromosome as described by Wilson ('05 and '06) and Montgomery ('06). Wilson's reëxamination of his preparations with additional studies on smear preparations and living material, led to the same conclusion as before. Lefevre and McGill ('08) have reëxamined the form and their results agree in every detail with those of Wilson and the later ones of Montgomery. From the

evidence at hand, there seems to be no doubt that Foot and Strobell were in some manner misled.

Boring ('07), in 22 species of Hemiptera homoptera, describes the accessory chromosome as univalent and dividing only in the second division.

The work of McClung, Sinety and Sutton on the Orthoptera, has been consistent in showing that the accessory chromosome arises from a single spermatogonial chromosome. In apparent contradiction to this interpretation are the results of Voinov ('04) on *Gryllus*, Montgomery ('05) on *Syrbula* and Zweiger ('06) on *Forficula*. Each of these observers describe the accessory chromosome as arising from the fusion of two spermatogonial chromosomes and dividing in both divisions. In opposition to Montgomery's work on *Syrbula* is the recent paper by Robertson ('08) on the same genus. He seems to demonstrate conclusively that the accessory chromosome is univalent and divides in only one division. Randolph ('08) in the earwig *Anisolabis*, describes an equal pair of idiochromosomes. May it not be possible that Zweiger mistook, in *Forficula*, such a pair of idiochromosomes for a bivalent accessory?

Montgomery ('05) also described the accessory chromosome of *Lycosa*, a spider, as bivalent and arising from the union of two spermatogonial chromosomes. While he did not determine definitely the manner of its division, he was inclined to believe that it divided in both divisions, judging from the manner of its formation. About the same time Wallace ('05) published her account of *Agalena*. She figured two accessory chromosomes which divided in neither division. In an attempt to unravel these contradictions, Berry ('06) describes the behavior of the chromosomes in *Epeira*. She shows conclusively that there is an odd number of chromosomes in the spermatogonia and that the accessory chromosome is a spermatogonial chromosome which retains its identity throughout the growth period and divides in only one division. This makes the results in spiders consistent with the majority of those in the Orthoptera and Hemiptera.

The results of Blackman on *Scolopendra* ('05) and Medes on *Scutigera* ('05) show that the accessory chromosome in the Myriapoda is a single spermatogonial chromosome, but each finds

the chromosome nucleolus of the growth period ("Karyosphere") made up of all the chromosomes.

McGill in her earlier work on *Anax junius* ('04) described the accessory chromosome as arising from a union of two small chromosomes as Paulmier had done in the case of *Anasa tristis*. The later paper of Lefevre and McGill ('08) on the same form, corrects the above error and shows that the accessory chromosome is a single spermatogonial chromosome.

The accessory chromosome in the Coleoptera as described by Stevens ('05, '06 and '09) arises from a spermatogonial chromosome and divides only in one division.

The idiochromosomes as described by Wilson ('05 and '06) for the Hemiptera, Stevens ('05 and '06) and Nowlin ('06) for the Coleoptera, and Stevens ('08) for the Diptera, are two univalent spermatogonial chromosomes which usually remain condensed throughout the growth period. They unite at synapsis in the Coleoptera and one chromosome nucleolus is present during the growth period except in *Tenebrio*, where the idiochromosome bivalent does not remain condensed. In the Hemiptera and Diptera they may or may not unite at the primary synapsis to form a bivalent body. In the former case, one chromosome nucleolus is present during the growth period, but separates into its univalent elements before the first maturation division. In the latter case, two chromosome nucleoli are present in the growth period.

The m-chromosomes as described by Wilson ('05), are two spermatogonial chromosomes which do not unite at the general synaptic period and which may or may not condense in the early growth period to form two small chromosome nucleoli. They undergo a late synapsis in the prophase of the first division to form a bivalent, which divides in both divisions.

We thus see that the three classes of chromosome nucleoli—namely, those derived from the accessory chromosome, from the idiochromosomes, and from the m-chromosomes, are alike in that all are direct descendants of spermatogonial chromosomes.

The differential chromosomes or chromosome nucleoli of the Reduviidae, which are described in the present paper, are in each case, with the possible exception of *Acholla ampliata*, univalent,

and derived from univalent spermatogonial chromosomes. The case of the large nucleolus of *Gelastocoris* is not so clear, but as previously stated, there is a possibility that the differential chromosomes are embedded in the nucleolus, although not as distinct and separate individuals as in the Reduviidae. The differential chromosomes in the Reduviidae, are without exception (as far as examined) embedded in a plasmosome. This plasmosome may be pale (*Prionidus*, *Sinea*) in which case the chromosomes stand out clearly, or it may stain rather densely (*Diplocodus*, *Conorhinus*) so that the chromosomes can be seen only faintly or not at all. In this respect they differ from the chromosome nucleoli formed by the accessory, m- and idiochromosomes. The accessory chromosome is, in the early part of the growth period, in contact with a pale plasmosome, but later separates from it. The idiochromosomes also may be associated during a part of the growth period with a plasmosome. The m-chromosomes may lie in any position and have no relation to the plasmosome.

Origin of the Differential Chromosomes.

In a study of the differential chromosomes, one of the most interesting questions which arises, is the origin of the asymmetrical chromosome distribution. It seems almost a certainty that these peculiar forms of distribution have not been present since the origin of the species, but have arisen sometime within its history.

In a discussion of this question, Montgomery ('06) is inclined to the belief that the m-chromosomes and idiochromosomes are not radically different structures, but are rather extremes of a series of modifications. Of their origin he says, "First a pair of autosomes (chromosomes) became modified so as to retain their compact nature during the growth period, still maintaining their approximate equivalence in volume. Because such allosomes are usually very small, we might conclude also, that they arose from the smallest pair of autosomes. In the next change would appear a growing disparity in size, which, if our last assumption be correct, would be due not to one becoming smaller and the other becoming larger, but rather to one retaining its original volume and to the other becoming much larger. This

second step would then be one of differentiation of the two, a becoming different, probably implying also difference of metabolic activities. This would account for the lessening affinity of the two as exhibited by the protraction of the time of conjugation. Then would be attained the stage of the second type of diplosomes (idiochromosomes), no longer united but separate in the first maturation spindle. And the last step would be that, instead of a reduction division of them in this spindle there would take place there an equational division of each." This conception is rendered untenable by Wilson's discovery that in *Metapodius* a typical pair of m-chromosomes and of unequal idiochromosomes coexist in the same species. In his papers of '01 and '05, Montgomery has argued that the accessory chromosome is bivalent and arose by some abnormality in mitosis as by the failure of two spermatogonial chromosomes to separate. Wilson ('05 and '06) suggests that the accessory chromosome may have arisen by the gradual disappearance of the small idiochromosome. Montgomery ('06) realizes this possibility, although he offers objections to it. While Wilson still believes that this interpretation may be applicable in many cases, in his work on *Metapodius* ('09b), he gives another possibility of its origin along with that of the supernumeraries. He says, "This was suggested by the observation that in a very few cases in 22 chromosome individuals, both idiochromosomes were seen passing to the same pole in the second division. The rareness of this occurrence shows that it is doubtless to be regarded in one sense as abnormal. But even a single event in an original 22-chromosome male, if the resulting spermatozoa were functional, might give the starting point for the whole series of relations observed in the genus, including the establishment of an unpaired idiochromosome. The result of such a division should be a pair of spermatozoa containing respectively 10 and 12 chromosomes. The former might give rise at once to a race having an unpaired idiochromosome and the somatic number 21 in the male. The latter might similarly produce an individual having in the first generation a single supernumerary chromosome and in succeeding generations an additional number."

In regard to the possible origin of the supernumeraries in

Diabrotica, where they are associated with an odd chromosome instead of a pair of idiochromosomes, Stevens ('08) makes the following suggestion: "It may be possible, as was surmised earlier in the study, that (1) there will prove to be two distinct types (varieties or species), in each of the present species, one having the large unpaired heterochromosome only; the other having an equal pair of chromosomes as in *Haltica*, and that (2) the irregularities in time of division and the consequent peculiarities in number and distribution of the supernumeraries in *Diabrotica* are to be attributed to hybridism."

The differential chromosomes in *Gelastocoris* and in the Reduviidae seem to have undergone a somewhat different history from that of the other types. It is clear that the single large idiochromosome of *Diplocodus* is represented in *Fitchia* by two chromosomes, in *Prionidus* and *Sinea* by three and in *Gelastocoris* by four chromosomes. It is very probable that the condition seen in *Diplocodus* is the most primitive one, and the essential question is how the other types can have been derived from this. Taking as an example *Fitchia*, where the female number is 28 and the male 27, if a pair of idiochromosomes was the original condition in the species, the original number of chromosomes must have been 26 in both male and female. If, in the male, the original large idiochromosome should break up into two parts, two classes of spermatozoa would be found, one containing 13 chromosomes and the other 14. All the eggs would have 13 chromosomes. If an egg were fertilized by a 14-chromosome class of spermatozoa, the result would be a female with 27 chromosomes. In maturation, this female would produce two kinds of eggs, one with 14 chromosomes and the other with 13. The 14-chromosome class fertilized by a spermatozoon with 13 chromosomes would produce either a male or female with 27 chromosomes. From these individuals, then, would arise both eggs and spermatozoa with 13 and 14 chromosomes. As the 14-chromosome class of spermatozoa would be female-producing, females with 28 chromosomes would be produced upon fertilization of an egg with 14 chromosomes by a spermatozoon with 14 chromosomes. Further, an egg with 14 chromosomes, fertilized by a spermatozoon with 13 chromosomes would produce a male with

27 chromosomes. This gives the number relations as we find them at present if the individuals with the original number (26) and the females with 27 disappear. The same explanation holds for the remainder of the types if we assume that the large idio-chromosome breaks up into three or four elements instead of two. Another thing which adds weight to the above interpretation is the fact that the behavior of each of the triad, tetrad and pentad groups, as a whole, is exactly comparable to the behavior of a pair of idiochromosomes. Evidently the original irregularity might have first occurred in either sex and have been transferred to the other. This gives another method by which the chromosome number may change during the history of the species. While *Metapodius* and *Diabrotica* are species where a change is actually taking place at the present time, the forms described in the present paper (with the exception of *Diplocodus*) show a fixed condition after a change has taken place.

Sex Determination.

In a preliminary note ('08) Morgan has given some interesting data in regard to sex determination in phylloxerans, where all the fertilized eggs produce females and where both males and females develop from parthenogenetic eggs. In describing the spermatogenesis he says: "The reduced number of chromosomes is three. In the first spermatocyte division two of these divide equally, but the third lags behind the others, and finally in the very last stages of this division, it retreats to one of the poles. Thus there are three chromosomes in one of the two daughter cells, and only two in the other. Still more significant is the fact that the cell with the fewer chromosomes is very small; it contains very little cytoplasm and subsequently degenerates without forming a spermatozoon. In the second spermatocyte division all three chromosomes of the larger cell divide equally, thus producing two spermatids with three chromosomes each. These spermatids become spermatozoa. They correspond in their mode of development to the 'female-producing' spermatozoa of other insects. Hence we can understand why all fertilized eggs become females."

To those who have sought to bring forward a theory of sex

determination of universal application, the parthenogenetic forms have been more or less of a stumbling block. The above results are in perfect harmony with the hypothesis of sex-production advocated by McClung, Stevens and Wilson.

Morgan also gives some further observations, indicative as to the manner in which males and sexual females are produced from parthenogenetic eggs. "I find that the somatic cells of the males of the species referred to above contain only five chromosomes. These five give in the spermatogenesis the reduced number three by two uniting with each other and the third having no partner. I find that the somatic cells of the female contain six chromosomes. It follows that at some time in the life cycle of the parthenogenetic eggs, one chromosome disappears in those eggs that become males, while the full number is retained in the female. It seems plausible that this change takes place in the formation of the single polar body given off by the parthenogenetic egg.

"The results seem to show that while the sex of the stem mother is connected with the presence of 'female-producing' spermatozoa, the production of males and of sexual females is dependent on a process that takes place in the egg analogous to the same process that takes place in the spermatogenesis of other kinds of insects. Hence it follows that the egg as well as the sperm has the power of determining sex by regulating the number of its chromosomes."

Von Baehr's recent results ('08) and also those of Stevens ('09) on the aphids confirm those of Morgan on the phylloxerans.

In a preliminary note ('08) Baltzer gives some results on echinoderm eggs, where he finds in the early cleavage stages of fertilized eggs of *Echinus microtuberculatus* and *Strongylocentrotus lividus*, an unpaired element which comes from the egg nucleus. Further, this unpaired element is present in only a part of the eggs. He suggests the possibility that this may be a chromosome which has to do with sex determination. If this element should prove to be a chromosome and in one half of the eggs, it would be the reverse of the condition found in the insects, for there the unpaired chromosome has arisen in the male. However, two such diverse phenomena are not impossible in different groups of animals, as we have no reason to suppose that

sex differentiation has taken place in the same manner in all animals. In fact, the quotation from Morgan shows that two classes of eggs are produced in phylloxerans and that the inequality of the chromosome distribution is accomplished in some manner at the time of the formation of the polar body.

McClung, Stevens and Wilson in their studies on the chromosomes of the insects have argued that the accessory chromosome and the idiochromosomes are either sex determinants or are in some manner connected with the determination of sex. The manner in which this is brought about yet remains a question. Wilson ('06) gives two interpretations by which the end result as we find it may be reached. First he follows out the earlier hypothesis of Castle ('03) that sex production may be interpreted as the result of a Mendelian segregation, transmission and dominance of the sexual characters. This interpretation involves two assumptions, neither of which have been proven, but which he argues may not be insuperable difficulties. One is the assumption that there are two kinds of eggs, the other, that selective fertilization occurs.

As an alternative point of view, he gives a second interpretation, in which he suggests that possibly the differential chromosomes may not be qualitatively different except in the degree of their special activity; or the end result may be due merely to a quantitative difference in the chromatin. Wilson, himself, in his work on *Metapodius* ('09), where the female may or may not have a larger amount of chromatin than the male, has brought forward evidence against the quantitative interpretation.

My results in the present paper offer nothing new in regard to the theory of sex determination, but are in perfect accord with the majority of previous results on the insects. I shall not venture far into theoretical discussions. There is, however, one question which naturally arises. Why do we have so few as one and two chromosomes involved in the production of males and females respectively in those forms with an odd chromosome, and as many as five and eight in *Gelastocoris*? This is not so strange, if the unequal distribution in these forms has arisen from a pair of idiochromosomes as previously explained. In every case whether the difference in number be one, two, three

or four, the female has the larger quantity of chromatin with the possible exception of *Acholla multispinosa*. Here the male seems to have the greater quantity and this inequality is brought about by the differential chromosomes themselves. This argues further against the interpretation that sex is determined by a quantitative relation of the chromatin.

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